Does size dimorphism reduce competition between sexes? The diet of male and female pine martens at local and wider geographical scales

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Sex-specific niche segregation is often used to explain sexual size dimorphism (SSD). However, whether food niche partitioning between sexes occurs as a case of sexual size dimorphism or by other mechanisms, such as behavioural dimorphism or habitat segregation, remains poorly understood. To evaluate the nature and extent of food-niche differentiation between sexes in a solitary predator I examined variation in the diet of male and female pine martens *Martes martes* Linnaeus, 1758 in years of high and low rodent abundance. Small mammals were the most important prey for pine martens in years of both low and high rodent abundance (occurring in more than 49% of scats). Birds, invertebrates and plant material were relatively common food items in summer diet, whereas ungulate carcasses were often consumed in autumn–winter. In general, males consumed more ungulate carcasses, plant material, amphibians and reptiles than did females, whereas females preyed more on squirrels and birds than males. There was significant seasonally dependent, between-sex variation in the occurrence of shrews, small rodents, other mammals, birds and invertebrates in marten diet. Whereas the occurrence of bank vole, birds, carcasses and plant material changed between sexes, seasons and years with various rodent abundances, both sexes consumed larger prey and had increased food niche breadth in years of low compared with high rodent abundance. Neither prey size nor food niche breadth were significantly different between males and females. The food-niche overlap between sexes was consistently lower in spring and in years of low rodent abundance. A wider geographical comparison of different marten populations showed that the diet of males and females varied significantly between locations. Females consistently preyed on squirrels and birds, whereas males fed more often on ungulate carcasses and plant material. Local and geographical comparison of male and female diets suggest that food-niche partitioning between male and female pine martens changes across different habitat and food conditions, and is not related to sexual size dimorphism, but rather to behavioural differences between sexes.

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Introduction

The number of individuals in a population is generally limited by resources and thus individuals should aim to secure resources for themselves, which in many cases requires the establishment of territories and exclusion of conspecifics (Adams 2001). In solitary carnivores, individuals of the same sex tend to be spatially separate; however, spatial overlap between the different sexes is often high (Powell 1979, 1994, Erlinge 1995). Therefore, exploitative competition between individuals of different sexes may be stronger than among individuals of the same sex. Furthermore, environmental conditions vary, and resources may be abundant within certain seasons or years but scarce and limited in others. Thus, the potential for competitive interactions are presumably more severe, and minimisation of the food niche overlap between sexes is more likely, as resource availability decreases (Wiens 1993). Both theoretical and experimental studies of intraspecific competition conclude that niche differentiation is necessary for the coexistence of individuals of both sexes in a population (Brown and Lasiewski 1972, Schoener 1974). However, the question of how individuals of different sexes separate their niches (mainly food-niche) and reduce competition is still under debate (eg McDonald 2002, Pearson *et al*. 2002).

Niche differentiation can arise through sexual differences in body size (morphological dissimilarity). Sexual size dimorphism (SSD) is widespread among mammals, where males are typically larger than females (Andersson 1994). This phenomenon has often been invoked in relation to two broad hypotheses: the niche variation hypothesis and the sexual selection hypothesis (Van Valen 1965, Shine 1989, Andersson 1994, Dayan and Simberloff 1994, Blondel *et al*. 2002). The niche variation hypothesis states that an increase in the diversity of the food resources used by a population leads to an increase of SSD resulting from differences between sexes in resources utilization (Van Valen 1965, Shine 1989, Dayan and Simberloff 1994). In populations with a wide food niche breath and/or feeding on a wide spectrum of prey size, the larger sex consistently takes larger and more diverse food items than the smaller one because they are adapted to handling larger prey (Shine 1989, Andersson 1994). Such niche differentiation is observed in many dimorphic animals (eg Erlinge 1979, Pearson *et al*. 2002). In British and Irish mustelids for example, the mean mass of mammalian prey taken by males was larger than that taken by females (McDonald 2002). Resource partitioning by size can also occur when the smaller sex has access to prey that is not available to the larger sex (Wilson 1975). If any morphological adaptation of males or females increases their ability to catch a certain type of prey (larger or smaller), this ability should be the same despite any variation of food conditions within or between populations.

In contrast to the niche variation hypothesis, the sexual selection hypothesis states that SSD in mammals, especially among carnivores, mainly results from mate competition among males, and bioenergetic constraints of reproduction among females (Erlinge 1979, Moors 1980). This hypothesis assumes that at high densities, frequent encounters among competing males favour the bigger and stronger males and in consequence SSD is larger. If this hypothesis implies SSD, observed food niche differences among competing sexes should arise as a secondary consequence of sexual size dimorphism (Holmes and Powell 1994, McDonald 2002) and/or they arise from other niche differentiation eg differences in habitat or microhabitat use, activity patterns, or foraging behaviour (behaviour dissimilarities). In some predators, strong sexual segregation has been found in activity patterns and habitat selection (Lodé 1999, Zalewski 2001, Marcelli *et al*. 2003). Females of the polecat *Mustela putorius* and pine marten *Martes martes* Linnaeus, 1758, for example, tend to be more diurnal than males, but the activity patterns of both sexes vary strongly among seasons and between individuals of the same sex with different reproductive status (Zalewski 2001, Marcelli *et al*. 2003). Therefore, in contrast to the morphological dissimilarities, the behavioural dissimilarities between sexes may change with variations in factors including food abundance or weather conditions (Zalewski 2001, Zalewski *et al*. 2004)

and as a result, the degree of food niche partitioning between sexes may also vary.

The European pine marten is a medium-size Mustelid characterized by high sexual size dimorphism across the species' geographic range; however, marten sexual size dimorphism is not related to the physiogeographic characteristics of the population (Reig 1992). Across a large spectrum of habitats, pine marten diet, food niche breadth and prey size vary in relation to habitat types and latitude (Zalewski 2004). In the northern part of the marten's range the resource base is more restricted and the food niche breadth is wider (Zalewski 2004). Within Białowieża Primeval Forest (E Poland) small rodents (primarily the bank vole *Myodes glareolus*) constitute the main prey of pine marten (Jędrzejewski *et al.* 1993). However, the populations of forest rodents in Białowieża Forest are subject to fluctuations driven by periodical heavy seed crops (Pucek *et al.* 1993, Jędrzejewska and Jędrzejewski 1998). Therefore, when rodents are not available, pine martens switch to alternative small prey, such as birds and amphibians, as well as larger prey (lagomorphs, larger birds) or ungulate carcasses (Jędrzejewski *et al.* 1993, Zalewski 2004). Such fluctuation in the abundance of the main prey type makes it possible to analyse variation in the niche overlap and prey size selection of both sexes according to resource availability, which is critical to understanding resource partitioning in predators.

The main purpose of this paper is to evaluate the nature and extent of food-niche differentiation between sexes in the pine marten, and to identify the potential mechanisms that might play a role in SSD in this solitary predator. The aims of this study were to: (1) analyse the differences in the diet of male and female pine marten and (2) examine food niche overlap between the sexes in seasons and years with high and low abundance of their main prey at a local scale, as well as (3) analyse the pattern of food-niche differentiation between males and females in various geographical regions of Central and Eastern Europe to determine whether there is regional specialisation and general patterns of diet partitioning between sexes. If SSD arises through niche partitioning I predict that: (1) males will

capture larger prey species more often than females due to their larger body size (at both local and geographic scales); (2) selection of a particular prey size by a given sex should not change under different food availabilities. Alternatively, if SSD relates to sexual selection the food-niche differentiation between sexes will change between periods of abundance and scarcity of rodents, or across various geographical locations as a result of variation in the behaviour of both sexes.

Material and methods

Study area

The study area was situated in north-eastern Poland (52°43'N, 23°54'E) in a strict reserve (47.5 km^2) of the Białowieża National Park (BNP) and surrounding forest located on the Polish-Belarusian borderland. BNP is part of a large primeval woodland covering over 1250 km^2, which represents the best preserved deciduous and mixed lowland forest in Europe. BNP is dominated by oak-lime-hornbeam forests (44.4% of the area), comprising principally of hornbeam *Carpinus betulus*, oak *Quercus robur* and lime *Tilia cordata*, as well as scattered spruce *Picea abies* trees. Other forest types include mixed coniferous (dominated by spruce and pine *Pinus silvestris*) and ash-alder (dominated by black alder *Alnus glutinosa* and ash *Fraxinus excelsior*) forest. Old-growth forests of BNP are characterised by multi-aged tree layers (mean age of tree stands 130 years), the presence of snags and fallen logs of large diameter, and small gaps in the canopy. The study area has not been exploited for timber, and human disturbance is very low, being restricted to the south-west part of the study area (mainly by pedestrian tourists). Pine martens coexist here within very rich communities of prey in addition to other predators (Jędrzejewska and Jędrzejewski 1998). No trapping or hunting of martens or other predators occurs.

The climate is transitional between continental and Atlantic types, although more continental conditions prevail (Olszewski 1986). During the study, the coldest month was either January or February with the lowest average monthly temperature (–8.5°C), and a maximum snow cover of 63 cm. The warmest month was July with an average monthly temperature reaching as high as 22.5°C. More detailed information about the study area is available in Jędrzejewska and Jędrzejewski (1998).

Body size

I used the body mass and body length of individuals live-trapped for radio-tracking (Zalewski and Jędrzejewski 2006) in BNP, along with specimens from collection of the Mammal Research Institute Polish Academy of Sciences in Białowieża, Poland, to estimate size dimorphism between

males and females. All specimens were collected between 1961 and 2005. Pregnant females were not included in this comparison.

Diet analysis

I studied the diet of marten by scats analysis of individuals of known sex obtained from two sources: (1) at the resting sites used by radio-tracked individuals and (2) during snow-tracking of these individuals. In Białowieża Forest, pine martens mostly use arboreal resting sites (Zalewski 1997a) and they position their latrines on branches near these sites (2–4 m away). Most of the scats were collected within trees at a height of 10–25 m. Scats that had fallen from arboreal latrines were also collected, though only when fresh so as to avoid misclassification of fox scats (Davison *et al*. 2002). Radio-tracking data showed that different individuals very rarely use the same resting sites (Zalewski 1997b). Scats were collected only from resting sites located close to the centre of home ranges to avoid collecting scats from different individuals. Additionally, material from resting sites that were known to have been occupied by individuals of both sexes was rejected.

Pine marten scats were air-dried, stored at room temperature and analysed following standard procedures (Jędrzejewski *et al*. 1993, Jędrzejewska and Jędrzejewski 1998). All food remains were separated and identified with the aid of keys (Böhme 1977, Pucek 1984) and the Mammal Research Institute Polish Academy of Sciences reference collection. As skeletal remains were often too fragmented to properly identify prey species, individual guard hairs were identified. Hairs were washed and cleaned in alcohol for 1–3 h, and guard hairs were identified according to cuticle scales and medulla patterns (Teerink 1991). Seeds of plants were compared with collections of seeds gathered in the study area. Diet composition was expressed in two ways: (1) as percentage of occurrence (%Occ) and (2) as percentage of the biomass consumed (%Bio). The percentage of occurrence in scats was defined as the number of scats with remains of a particular prey compared with the total number of scats (taken as 100%). The percentage of fresh biomass consumed was obtained by weighing all dry food remains and then multiplying by the corresponding coefficient of digestibility (insectivores and small rodents 23; medium sized mammals 50; wild boar 118; deer 15; birds 35; amphibians and reptiles 18; fish 25; insects 5; fruit, seed and other plant material 14 – Jędrzejewska and Jędrzejewski 1998).

Marten diet was analysed using data from three seasons and high-moderate and low abundances of rodents. Seasons were defined according to the biology of martens: spring (pregnancy, birth and rearing of cubs); summer (rearing of cubs and mating season); autumn-winter (solitary life and dispersal of young) (Grakov 1981). An index of abundance of forest rodents, combining the bank vole and the yellow-necked mouse *Apodemus flavicollis*, was obtained by removal trapping in the study area three times per year (Pucek *et al*. 1993, Stenseth *et al*. 2002). The observed indexes of rodent density were categorised as low (0.1–0.3 rodents/100 trap-nights (TN) in spring, 0.4–0.9 in summer and autumn), high-moderate (0.6–2.6 rodents/100 TN in spring, 2.0–13.4 in summer and autumn). The years

of moderate and high rodent densities were combined due to only one observed year of high rodent densities. I used log-linear analysis of the frequency of prey occurrence data to test the dietary differences between sexes during the three seasons and the two periods of rodent abundance. I did not use the Bonferroni correction of the alpha level because this approach has been increasingly criticized by statisticians and ecologists in recent years as being too conservative (eg Moran 2003).

The standardised food niche breadth using Levins index and the trophic niche overlap using the Pianka index were calculated for 9 food categories (Krebs 1989). The following food taxa categories were used in comparative analysis of diet composition of both sexes: (1) shrews, (2) small rodents, (3) squirrels, (4) other medium size mammals, (5) birds, (6) carcasses, (7) other vertebrates (reptiles, amphibians and fish), (8) invertebrates, and (9) plant material (fruits, seeds and grass etc., including fungi). The variation in food niche breadths and niche-overlap indexes were compared using general linear models (GLM).

An index of prey size in pine marten diets was calculated according to Erlinge's (1987) formula: (Σ the mean mass of each prey categories x the proportion of occurrence of that prey categories in the diet)/number of categories. The following body mass categories of prey item were used: shrews – 10 g, small mammals – 25 g, red squirrels *Sciurus vulgaris* – 230 g, hares *Lepus* spp. – 1500 g, other medium-size mammals (weasel *Mustela nivalis*, mole *Talpa europaea*, hedgehog *Erinaceus concolor*) – 100 g, small birds – 30 g, large birds – 500 g, amphibians and reptiles – 15 g, insects – 3 g, and ungulate carrion – 200 g. Martens only ate juvenile hedgehogs, and I therefore assumed the average size as 100 g. I assumed that the weight of carrion consumed by martens corresponded to the maximal capacity of their stomach (Grakov 1981).

Microhabitat use

Data on foraging modes of males and females in winter were obtained from snow-tracking of radio-marked individuals. All activities of the snow-tracked individual, including hunting events and the selection of habitat structures (eg fallen logs, trees) along 250-m of marten trails were registered.

Review of published data

To calculate diet variation between sexes in various geographical locations, I collected all available literature on the diet of European pine martens and selected those that met the following criteria: (1) the diet composition was estimated by the analysis of stomachs and/or scats with a minimum sample size per sex of more than 20 stomachs or scats; (2) the study was carried out in winter (winter is the most food limited season – Zalewski 2004); and (3) the main food categories were described including medium size mammals. The data from Pechora river, Russia were presented separately due to large differences in the diet which may suggest that samples were collected from different populations. The percentage of occurrence in scats/stomach is the most commonly used method in diet analysis so I used this in my

comparisons. The food items were reclassified into the 9 food categories described earlier and the mean prey size was calculated using the same food categories and formula as in the Białowieża study. Statistical differences between populations and sexes were assessed using log-linear likelihood tests of the frequency of occurrence.

Results

Size dimorphism

Pine martens showed marked sexual size dimorphism in Białowieża, with males being significantly larger than females in both body mass and length (Table 1). Sexual size dimorphism reached 41% in body mass and 11% in body length.

Variation in diet composition

I analysed 697 scats from 8 males and 506 scats from 8 females. Small mammals, particularly bank voles and yellow-necked mice were the most important prey in years of both scarce and moderate-high rodent abundances (ie they occurred in over 49% of the scats and constituted over 30% of the consumed biomass; Table 2, Fig. 1). Birds, invertebrates and plant material were a relatively common food source in summer, whereas ungulate carcasses were mainly consumed in autumn-winter (Table 2, Fig. 1).

There was a significant difference between the sexes in the frequency of all food categories (except *Apodemus* spp.) in the diet (Table 2 and 3). Males ate more amphibians and reptiles whereas females preyed more on squirrels. There were significant three-way interactions for each of the five prey categories (shrews, small rodents, other mammals, birds, and invertebrates) with season and sex (Table 3). This implies that the occurrence of rodents in scats was significantly lower for males than females in summer and autumn-winter, but higher in spring. In contrast, males consumed more invertebrates than females in summer, but not in spring. In spring and autumn-winter, shrews and birds were consumed more often by females than by males. Furthermore, there were significant three-way interactions between birds, rodent abundance and sex (Table 2 and 3). When rodent abundances were moderate-high, female martens ate more birds, whilst males fed on birds more often when rodent abundances were low. The frequency of occurrence of three food categories (bank voles, carcasses and plant material) varied between sexes, seasons and years of rodent abundance (Table 2 and 3). In years of high rodent abundance, males ate more bank voles in autumn-winter, whereas females ate more bank voles in summer and autumn-winter when rodent abundance was low. Males generally consumed more from ungulate carcasses than did females, although females utilised this resource to a similar level in summer and autumn-winter during years of low rodent abundance. In general, plant material was eaten more often by males, especially in summer in high-moderate rodent abundance years, in contrast to summers of low rodent abundance when plant material was eaten more often by females (Table 2 and 3).

The prey size index varied between 4 and 16, and the GLM for the prey size index against season, sex and rodent abundance was significant ($F_{4,11} = 12.4$, $p = 0.003$; Table 2). In the winter and in years of low rodent abundance, marten diet was composed of a greater amount of larger

Table 1. Body measurements of pine martens from Białowieża Forest (data pooled from 1961–2005). The significance of differences between males and females was calculated by *t*-test.

Measurements	Males		Females		*t*-test	*p*
	n	Mean (SD)	*n*	Mean (SD)		
Body mass (kg)	23	1.36 (0.16)	17	0.96 (0.07)	9.39	< 0.0001
Body length (cm)	18	46.0 (1.84)	15	41.3 (1.45)	7.63	< 0.0001
Tail length (cm)	18	23.0 (1.47)	15	20.2 (1.47)	5.78	< 0.0001

Table 2. Variation in the diet of male and female pine martens *Martes martes* in years of low and high rodent abundance in the Białowieża Forest. Diet composition was calculated as the percentage of occurrence (%). Other small rodents – *Sicista betulina*, *Micromys minutus*; other mammals – *Lepus* sp., *Mustela nivalis*, *Erinaceus* sp., *Talpa euroapea*; M – males, F – females.

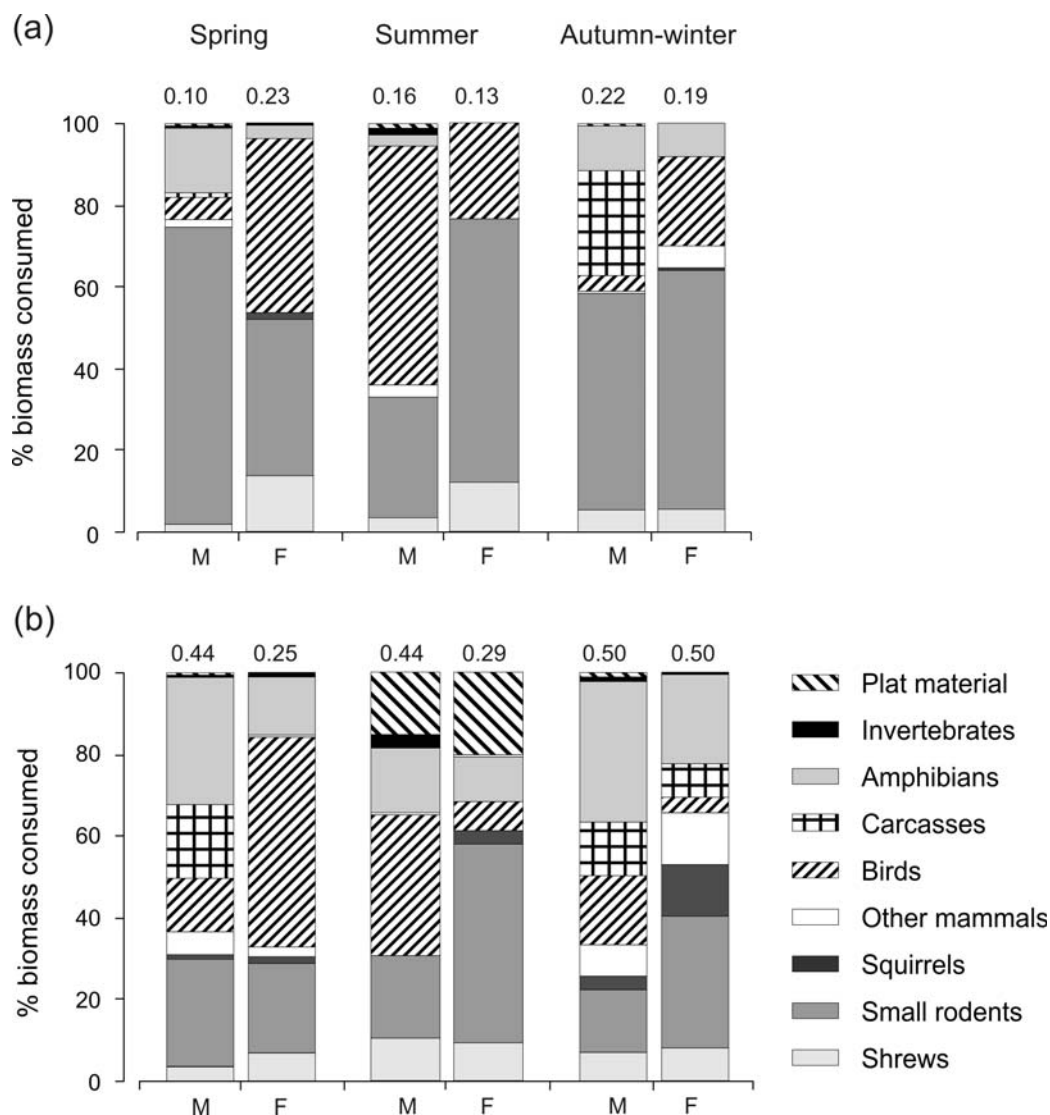| Food items	High-moderate rodent abundance						Low rodent abundance					
	Spring		Summer		Autumn-winter		Spring		Summer		Autumn-winter	
	M	F	M	F	M	F	M	F	M	F	M	F
Shrews	3.9	42.4	14.3	26.7	16.2	19.6	15.5	25.7	20.7	28.9	18.4	19.1
Clethrionomys glareolus	23.5	28.8	22.4	26.7	49.1	40.2	27.2	25.1	11.0	40.0	12.2	27.2
Apodemus spp.	9.8	8.5	10.2	13.3	10.2	2.2	5.8	4.8	9.8	0	16.3	13.2
Microtus spp.	47.1	15.3	14.3	40.0	10.2	42.4	12.6	9.6	6.1	26.7	3.4	3.7
Other small rodents	9.8	8.5	4.1	40.0	7.4	5.4	6.8	7.2	3.7	13.3	0.7	4.4
Small rodents total	82.4	59.3	40.8	80.0	69.0	82.6	46.6	42.5	29.3	73.3	32.0	44.9
Squirrels	2.0	1.7	0	0	0.9	3.3	1.0	3.6	0	2.2	3.4	12.5
Other mammals	4.0	0	8.2	0	2.8	9.7	7.8	7.8	0	2.2	8.8	18.3
Carcasses	9.8	5.1	1.0	0	46.8	6.5	46.6	7.2	3.7	2.2	42.2	37.5
Birds total	11.8	66.1	49.0	53.7	7.9	23.9	31.1	68.9	46.3	8.9	25.2	14.0
Reptiles, amphibians	27.5	10.2	10.2	0	26.4	21.7	34.0	20.4	23.2	33.3	45.6	36.8
Carabid beetles	17.6	3.4	37.8	0	3.2	1.1	16.5	31.7	15.9	11.1	8.2	0.7
Wasps and wild bees	0	18.6	16.3	0	1.9	2.2	4.9	0.6	43.9	13.3	17.0	2.9
Invertebrates total	21.6	39.0	63.3	0	9.7	9.8	28.2	46.1	69.5	28.9	32.7	15.4
Fruits	0	0	9.2	6.7	0.5	2.2	1.9	0.6	36.6	0	4.1	0
Nuts and seeds	2.0	5.1	3.1	0	2.8	0	5.8	2.4	2.4	60.0	9.5	2.2
Plant material total	7.8	5.1	21.4	6.7	5.6	3.3	13.6	6.0	46.3	62.2	15.6	2.2
No. of scats analyzed	51	59	98	15	216	92	103	167	82	45	147	136
Mean mass of prey	6.7	5.6	4.0	4.1	13.1	10.4	15.1	7.4	5.3	4.2	15.9	15.2

Fig. 1. The diet composition (% of consumed biomass) of male (M) and female (F) pine martens *Martes martes* in different seasons, and in periods of high-moderate rodent abundance (a) and low rodent abundance (b) in Białowieża Forest. Numbers indicate food niche breadth values.

prey than in other seasons or at higher rodent densities (season: $F_1 = 19.6$, $p = 0.001$; rodent abundance: $F_1 = 7.1$, $p = 0.031$ respectively). In all periods, however, both sexes consumed prey of similar size ($F_1 = 3.2$, $p = 0.114$).

Food-niche breadth and food-niche overlap

The food niche breath varied between 0.10 and 0.50 (Fig. 1). The overall GLM for food-niche breadth in response to season, sex and rodent abundance was significant ($F_{4,11} = 8.06$, $p = 0.009$). However, only the effect of rodent abundance was significant ($F_1 = 26.98$, $p = 0.001$), whilst season and sex were not ($F_2 = 2.09$, $p = 0.193$, $F_1 = 1.07$, $p = 0.335$, respectively). Both sexes had a wider food-niche in years of low rodent abundance. The food-niche overlap between sexes was consistently lower in spring and in years of rodent scarcity (GLM, $F_{3,5} = 95.37$, $p = 0.010$; season $F_2 = 130.67$, $p = 0.008$, and rodent abundance $F_1 = 24.77$, $p = 0.038$; Fig. 2).

Table 3. Summary of the log-linear analyses of the variation in the diet composition of male and female pine martens in three seasons and years of low and high rodent abundance from Białowieża Forest. Details are only given for terms that were found to be significant in the final models.

Food item	Effect	df	χ^2	p
Shrews	season * sex	2	10.28	0.01
Bank voles	season * sex * rodent abund.	2	7.30	0.03
Apodemus spp.	season * rodent	2	9.78	0.01
Small rodents	season * sex	2	33.51	< 0.0001
Squirrels	sex	1	12.86	0.0003
Other mammals	season * sex	2	11.25	0.004
Carcasses	season * sex * rodent abund.	2	13.74	0.001
Birds	season * sex	2	64.97	< 0.0001
	rodent * sex	1	27.57	< 0.0001
Amphibians and reptiles	sex	1	7.68	0.01
Invertebrates	season * sex	2	47.67	< 0.0001
Plant material	season * sex * rodent abund.	2	7.93	0.02

Foraging pattern in winter

In their search for prey, pine martens preferentially utilised fallen logs and root plates of fallen trees rather than standing trees (Table 4). Both males and females used fallen logs, root plates and visited cavities and holes near the ground with the same intensity. Females, however, climbed standing trees more often than males (Table 4). There was also evidence showing that females travelled longer distances in the tree canopy, although this was not statistically significant. Snow-tracking revealed that males attacked prey more frequently than females (Table 4).

Variation in male and female diets in Europe

The data on winter diet composition of male and female pine martens were available for 6 different populations in Central and Eastern Europe (Table 5). The diet of males and females varied significantly between locations (Table 5 and 6). The mean percentages of occurrence of
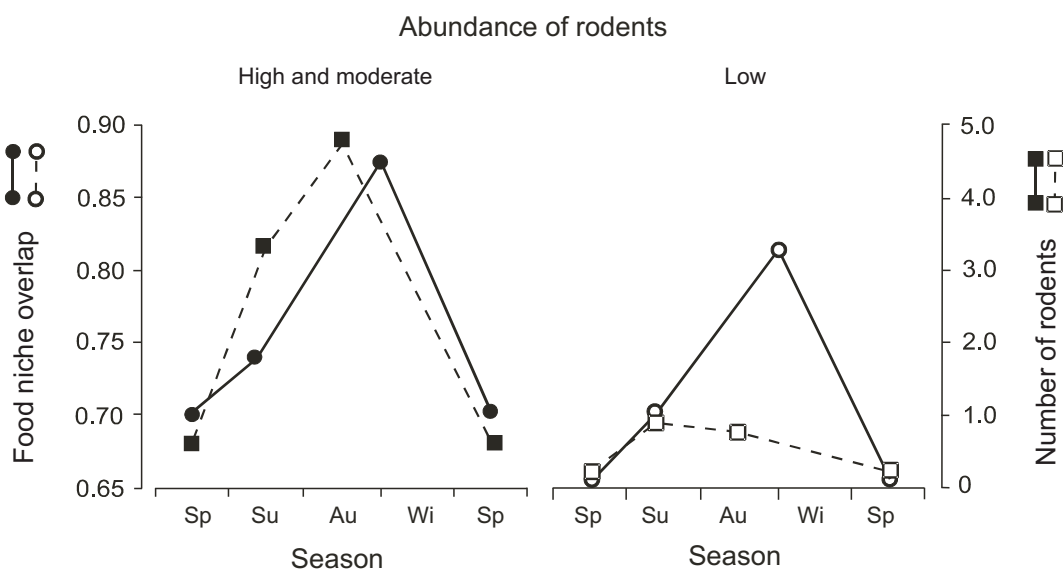

Fig. 2. Food niche overlap between male and female pine martens in relation to rodent abundance in periods of high-moderate and low rodent abundance in Białowieża Forest. Sp – spring, Su – summer, Au – autumn, Wi – winter.

Table 4. Foraging modes of male and female pine martens in the snowy period as revealed by snow-tracking of radio-marked individuals in Białowieża Forest. Number of 250 m of trails snowtracked: male – 17, female – 11. The significance of differences between males and females was calculated by t-test.

Parameter	n/250 m trail		t-test	p
	Male	Female		
Walking:				
along fallen log and root plate of fallen tree	0.23	0.64	1.43	0.163
under fallen log or branches	2.47	2.91	0.45	0.658
on log and root plate of fallen tree	8.29	9.09	0.47	0.642
Penetrating the cavities or hollow tree	0.06	0.18	1.87	0.072
Climbing standing growing tree	0.23	0.91	2.37	0.025
Number of attacks and foraging	1.00	0.09	−2.23	0.034
Distance travelled in tree canopy (m)	3.4	18.3	1.10	0.301

shrews, other vertebrates and invertebrates taken by both sexes were similar. In all populations, the females often preyed on red squirrels and birds, whereas males more often ate ungulate carcasses. There was a significant three-way interaction between two food categories (small rodents and plant material) sex and location (Table 6). This implies that in some populations, males hunted rodents significantly more often than females, whereas the opposite was true for other populations. The mean prey size in marten diets varied between populations but not between sexes ($F_5 = 92.1$, $p = 0.0001$, $F_1 = 0.43$, $p = 0.54$, respectively; Table 5).

Discussion

The niche variation hypothesis predicts that populations occupying broader ecological niches are expected to be more variable in phenotype than narrower-niched populations, and males, which are larger than females, will eat bigger prey than females (Van Valen 1965, Shine 1989). Contrary to this expectation at both local and geographical scales, despite being heavier than females, males did not consistently utilise larger prey than females. The dimorphism in prey size in male and female diets and food niche partitioning depended on rodent abundance and geographic locations. In the Pechora river region of Russia, one study revealed prey size in the diet of male martens was on average larger,

whereas another study in the same region found that on average prey size was larger in the diet of female martens (Yurgenson 1947, Yazan 1970). Similarly conflicting results have been reported for various Mustelids. In some species, males consumed larger prey than females (Birks and Dunstone 1985, Poole and Graf 1996, Birks and Kitchener 1999, McDonald *et al.* 2000, Sliva 2006); both sexes had a similar diet (McDonald *et al.* 2000, Lode 2003); or females consumed larger prey than males (Weber 1989). All these studies show a large variation in prey size selection by both sexes in various ecological scenarios, despite the fact that males are always larger then females. This suggests that neither food composition nor prey size alone explain the direction of size dimorphism in the pine marten.

Resource partitioning by prey size can also occur when the smaller sex has access to prey not available to the larger sex (Wilson 1975) and/or when a smaller body size increases hunting success. Squirrels are probably too agile to be easily captured by martens. However, in contrast to the heavier males, smaller female martens can jump from thinner branches, across larger gaps in the tree crown and as such may be able to follow and capture squirrels in the tree canopy. In all studies reviewed a higher proportion of squirrels was observed in female than male diet. SSD potentially reduces intraspecific resource competition between the sexes; however, it explains only a small part of the differences between male and female diet com-

Table 5. Winter diet composition of male and female pine martens (*Martes martes*) from various locations in Europe. Diet composition expressed as percentage of occurrence of prey items. °N – Latitude, °E – Longitude, *n* – number of stomachs or scats, Prey groups: Shrews – small insectivores, Rodent – small rodents, Squirr – squirrel, Other mamm – other mammals (*Lepus* spp., *Mustela* spp., *Talpa europaea*), Carcass – carcasses, Birds, Other vertebr – other vertebrates (amphibians, reptiles, fish), Inver – invertebrates, Plant – plant material (fruits and seeds) including fungi . Mean prey size calculated using Erlinge (1987) formula. * – Mean prey size calculated without grouping birds by size. Sources: 1 – This study, 2 – Mozgvoi (1971), 3 – Gribova (1958), 4 – Estafeva (1998), 5 – Yazan (1970), 6 – Yurgenson (1947).

Country, locality	Location		Sex	*n*	Percentage of occurrence in marten diet									Mean prey mass	Source
	°N	°E			Shrews	Rodent	Squirr	Other mamm	Carcass	Birds	Other vertebr	Invert	Plant		
Poland, Białowieża Forest	52	24	M	363	17.1	54.0	1.9	5.5	42.7	14.9	34.2	19.0	9.6	15.2	1
			F	228	19.3	60.1	8.8	10.5	25.0	18.0	30.7	13.2	2.6	15.6	
Russia, Bashirskii Reserve	54	57	M	564	52.5	75.2	1.1	2.3	0	9.0	0.2	11.2	1.8	5.4*	2
			F	252	49.2	67.5	1.2	3.2	0	16.3	0	8.3	1.2	5.6*	
Russia, Vologodtskoi region	60	40	M	114	17.5	43.9	6.1	19.3	0	20.2	7.0	0	16.7	30.8	3
			F	66	24.2	34.8	6.1	22.8	0	34.8	10.6	0	16.7	34.4	
Russia, North-eastern region of European part of Russia	61	50	M	130	6.1	48.5	16.2	0	0	27.7	6.2	0.8	30.0	14.1	4
			F	76	9.2	42.1	23.7	0	1.3	26.3	2.6	2.6	22.4	13.0	
Russia, Pechora river	62	59	M	86	3.5	48.8	17.4	0	3.5	30.2	15.1	0	38.4	17.5	5
			F	36	8.3	52.8	11.1	0	2.8	41.7	11.1	0	25.0	15.5	
Russia, Pechora river	62	59	M	43	4.6	14.0	48.8	0	0	30.2	0	4.7	4.7	28.4	6
			F	21	4.7	33.3	52.4	0	0	47.6	0	23.8	28.6	30.9	
Average			M		16.9	47.4	15.3	4.5	7.7	22.0	10.4	5.9	16.9	18.6	
			F		19.2	48.4	17.2	6.1	4.8	30.8	9.2	8.0	16.1	19.2	

Table 6. Summary of the log-linear analyses of the variation in the diet composition of male and female pine martens from various locations in Europe.

Food item	Effect	df	χ^2	p
Shrews	location	5	342.4	< 0.0001
	sex	1	0.2	0.666
	location * sex	5	4.3	0.500
Small rodents	location	5	149.9	< 0.0001
	sex	1	0.6	0.428
	location * sex	5	12.1	0.033
Squirrels	location	5	202.1	< 0.0001
	sex	1	6.3	0.012
	location * sex	5	10.7	0.057
Carcasses	location	5	530.8	< 0.0001
	sex	1	16.4	< 0.0001
	interaction	5	4.5	0.473
Birds	location	5	76.4	< 0.0001
	sex	1	12.3	0.0004
	location * sex	5	5.5	0.361
Other vertebrates	location	5	391.2	< 0.0001
	sex	1	0.8	0.380
	location * sex	5	2.2	0.820
Invertebrates	location	5	98.5	< 0.0001
	sex	1	2.0	0.158
	location * sex	5	9.1	0.107
Plant material	location	5	214.3	< 0.0001
	sex	1	5.6	0.018
	location * sex	5	16.2	0.006

position. Thus, the differences between male and female diet are certainly not the primary cause of sexual dimorphism. The questions remain: what caused the observed differences in diet composition between sexes and how do both sexes reduce food competition?

The coexistence in a competitive equilibrium can be maintained in several ways that include the use of different foraging techniques, having dissimilar activity patterns, or separate foraging habitats (Moors 1980). These behavioural differences may relate to the fact that large males dominate the smaller females, which tend to avoid encounters with males in the overlapping area of their territories (Erlinge 1979, Moors 1980). Under some conditions, males may monopolise and prevent female access to resources by forcing females to change their habitat use or activity pattern. Such exclusion has been observed in many birds, where smaller females are excluded from foraging habitats by larger males (Peters and Grubb 1983, Catry et

al. 2006). On the other hand, between-sex, spatially dynamic interactions indicated neither attraction nor active avoidance outside the mating season (Zalewski and Jędrzejewski 2006). This could support the hypothesis that sexes may independently change their hunting behaviour and mode of area searching, or habitat use, but that this might depend, on eg the reproduction effort or metabolic needs of the individual.

In general, male and female martens occupy overlapping home ranges (eg Marchesi 1989, Balharry 1993), but in Białowieża deciduous forest the home range overlap between sexes was relatively small (9% in autumn-winter and 27% in spring-summer; Zalewski and Jędrzejewski 2006). In marten populations inhabiting rich Białowieża forests, and thus reaching high densities, competition was reduced by decreasing the overlap of home ranges between sexes. Males used larger home ranges and their movements were longer and spread over a much larger area than female routes (Zalewski et al.

2004, Zalewski and Jędrzejewski 2006). By occupying larger home ranges, males may have a higher probability of finding certain food types, especially those trophic resources which are patchily distributed, such as fruits or ungulate carcasses. Throughout the marten's geographical range, the general pattern of males feeding more often on carcasses and plant material may be explained by their larger home ranges, as suggested for the fisher *Martes pennanti* (Giuliano *et al.* 1989). Males seem to engage in food gathering behaviour more often than females.

Variation in habitat use by males and females may cause the observed differences in diet composition (eg Erlinge 1979, Birks and Dunstone 1985). In Białowieża Forest, although they used similar habitats (A. Zalewski and K. Stachura- -Skierczyńska, unpubl.) males and females utilised different microhabitats with females climbing trees, travelling longer distances in the tree canopy, and investigating cavities slightly more often than males. This more arboreal behaviour of females may explain the larger proportion of birds in female diets, not only in Białowieża Forest, but also across wider pine marten geographical range (Table 5, and Marchesi 1989), as well as in the American marten *Martes americana* (Nagorsen *et al.* 1989). In Białowieża Forest, increased occurrence of birds in male summertime diet relative to females could relate to a higher number of fledglings in the forest at this time. The inexperienced young birds often rest on the ground or in shrubs (especially after rain) and are then easy to capture by males, mostly moving at ground level.

Circadian time segregation may also affect the variation in diet composition between sexes. In Białowieża Forest, males and females showed different rhythms of activity, especially in spring (Zalewski 2001) when females were more active than males during daylight (between 10.00– –16.00 h) and hunted more birds. As martens probably locate birds by sound (Jędrzejewski *et al*. 1993), the probability of catching a bird increases in daylight. In summer, males were slightly more active during daylight (especially in the early evening) (Zalewski 2000) and this may also contribute to the higher proportion of birds in male diet during that period. There-

fore, changes in the daily activity patterns of both males and females can facilitate prey partitioning.

A decline in food abundance resulted in wider food niches between the sexes in both pine and American martens (eg Thompson and Colgan 1990, Jędrzejewski *et al.* 1993). In American martens, only limited differences in diet choice between the sexes were observed during various seasons or years, including years of low food abundance (Thompson and Colgan 1990). In Białowieża Forest, a decline in rodent abundance together with an increase in the niche breadth of both male and female martens caused a slight decrease in niche overlap consistently throughout the seasons. This means that in years with low prey abundance, both sexes shifted toward different alternative preys with males feeding more on carcasses, frogs and fruits, and females concentrating on rodents and squirrels.

In conclusion, the data support the hypothesis that sexual dimorphism is more likely to be caused by different selective forces acting on the sexes separately (Moors 1980). In pine martens, between-sex resource partitioning is dynamic, arising from variation in several niche dimensions (behavioural dissimilarity in activity pattern, microhabitat use or space use) and is moderated by rodent abundance. Generally, females have smaller home range and used three habitat dimensions (ground level and within trees), whereas males had large home ranges and gathered more food types. The SSD in pine martens contributes to food niche partitioning as small females have easier access to arboreal prey than males. Altogether, these behavioural and morphological niche separations may provide females with sufficiently advantageous access to certain resources to reduce food competition with males.

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